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Metamorphosis and homology of mouthparts in Neuropteroidea (Hexapoda: Metabola), with remarks on systematics and nomenclature

Метаморфоз и гомология ротовых частей у Neuropteroidea (Hexapoda: Metabola), с замечаниями по систематике и номенклатуре

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KEY WORDS: Neuroptera, Planipennia, Neuropteroidea, Euneuropteroidea, Birostrata, Chrysopidae, Myrmeleontidae, Megaloptera, Rhaphidioptera, *Raphidia*, Meganeuroptera, *Sialis*, Eumegaloptera, maxilla, mandible, metamorphosis, larva, pupa.

КЛЮЧЕВЫЕ СЛОВА: Neuroptera, Planipennia, Neuropteroidea, Euneuropteroidea, Birostrata, Chrysopidae, Myrmeleontidae, Megaloptera, Rhaphidioptera, *Raphidia*, Meganeuroptera, *Sialis*, Eumegaloptera, максилла, мандибула, метаморфоз, личинка, куколка.

ABSTRACT. Examination of larval/pupal transformation in *Chrysoperla carnea* and *Chrysotropia ciliata* allows to understand homology of the larval paired piercing-sucking stylets, whose presence is the single known autapomorphy of Birostrata (= Euneuropteroidea s.str.). The maxillary component of the piercing-sucking stylet is formed by maxillary palp fused with galea, lacinia and a distal portion of stipes; its piercing apex is formed not by lacinia or galea, but by the maxillary palp. Piercing apex of the mandibular component of the stylet is not the mandibular incisor, but an outgrowth laterad of the incisor. Larval/pupal transformation of maxillae and mandibles in *Raphidia* and *Sialis* (as Neuropteroidea with primitively biting larval mouth apparatus) is described. A new circumscriptional name Birostrata, **taxon nov**. is introduced. Circumscriptional names Neuropteroidea, Neuropterida, Euneuropteroidea, Planipennes, Planipennia, Neuroptera, Rhaphidioptera, Raphidioptera, Meganeuroptera and Megaloptera are discussed. Neuropteroidea is probably a holophyletic taxon characterized by presence of imaginal dorsal stomodeal diverticulum and other autapomorphies.

РЕЗЮМЕ. Изучение личиночно-куколочной трансформации у *Chrysoperla carnea* и *Chrysotropia ciliata* позволило понять гомологию личиночных парных колюще-сосущих стилетов, наличие которых является единственной известной аутапоморфией Birostrata (= Euneuropteroidea s.str.). Максиллярный компонент колюще-сосущего стилета образован максиллярным щупиком, слитым с галеей, лацинией и дистальной частью стипеса; его колющая вершина образована не лацинией или галеей, а максиллярным щупиком. Колющая вершина мандибулярного компонента этого стилета — не мандибулярный инцизор, а вырост латеральнее инцизора. Описана трансформация максилл и мандибул при превращении личинки в куколку у *Raphidia* и *Sialis* — Neuropteroidea с исходным грызущим личиночным ротовым аппаратом. Вводится новое объёмное название Birostrata, **taxon nov**. Обсуждаются объёмные названия Neuropteroidea, Neuropterida, Euneuropteroidea, Planipennes, Planipennia, Neuroptera, Rhaphidioptera, Raphidioptera, Meganeuroptera и Megaloptera. Вероятно, Neuropteroidea — голофилетический таксон, характеризующийся наличием имагинального дорсального дивертикула стомодеума и другими аутапоморфиями.

Introduction

Since strict rules on circumscriptional names are elaborated [Kluge, 1999a, 1999b, 2000, 2004], it becomes possible to bring in order existent not-typified names which formerly were used differently by different authors. The most complete catalogue of these names is available from Internet [http://www.bio.pu.ru/win/entomol/KLUGE/nom/~~~Cont.htm]. However, a large generally accepted holophyletic taxon known under names “Neuroptera”, “Planipennia”, “Megaloptera” and

others, appears to have no correct circumscriptional name, which could be accepted; here for this taxon is proposed a new name Birostrata.

The only recently known reliable autapomorphy of Birostrata is a highly specialized structure of larval mouth apparatus, which represents a pair of composite piercing-sucking stylets. Mandibles and maxillae, which constitute these stylets, are so modified, that till now homology of their parts was unclear. In larvae of other Neuropteroidea — Rhaphidioptera, Sialis/fg1 and Eumegaloptera — mouthparts are not so modified, but homology of their maxillary parts also was a subject of discussion. For insects which undergo metamorphosis, homology of external parts of the body can be discovered if this homology is known for another stage of ontogenesis of the same insect: in this case it is possible to trace development of this organ during metamorphosis. For example, this method allowed to clarify homology of parts of imaginal maxilla in Aphaniptera [Kluge, 2002].

In all Neuropteroidea including Birostrata, homology of mandibular and maxillary parts is quite clear in pupa and imago, as pupal-imaginal mandibles and maxillae have structure close to the ancestral for Hexapoda. The aim of this work was to trace development of maxillae and mandibles from larva to pupa, in order to clarify homology of their parts in larva.

Below, some comments are given about general structure of maxillae and mandibles.

MAXILLA. One of the good autapomorphies of Hexapoda is structure of maxilla [Kluge, 1999b, 2000]. Basal portion of maxilla normally has only one wall — ventral (originally posterior), which is divided into two sclerites — cardo and stipes; from the stipes arise three projecting parts of maxilla — lacinia, cardo and palp. The palp is initially 5-segmented (but in some Hexapoda can have more or less than five segments). Maxilla has following muscles (Figs 18–20): stipital-cranial; muscles going from cardo and stipes to head endoskeleton (in Amyocerata — cardinal-tentorial and stipital-tentorial); lacinial-cranial, passing dorsad (originally anteriad) of all other muscles; lacinial-stipital; galeal-stipital and palpal-stipital, both passing ventrad (originally posteriad) of the lacinial-stipital muscle; intrinsic muscles of palp segments. Among Hexapoda musculature of maxilla is very conservative, and in many cases allows to clarify homology of parts of maxillae [Kluge, 2002]. During metamorphosis maxillary musculature can disappear completely (in Birostrata) or partly (in *Sialis* and *Raphidia*), but in all cases larva and imago have the same set of muscles peculiar for Hexapoda.

MANDIBLE. The initial mandible of Mandibulata has incisor (or apical canine), kinetodontium (or subapical canine) and mola [Kluge, 2000, 2004]. Some authors confused kinetodontium with prostheca (fused setae between kinetodontium and mola in some insects). In many insects kinetodontium is indistinguishable among secondary biting denticles. In many carnivorous insects mola is lost. Apex of incisor usually represents apex of the whole mandible. Initially, mandible has muscles going from its base to cranium (anterior abductors and posterior adductors) and to endoskeleton (in Amyocerata — to tentorium). In Metapterygota mandibular base is diminished, and mandibular-tentorial muscles are reduced, often completely lost.

1. Neuropteroidea

Circumscriptional names:
Neuropteroidea Handlirsch, 1903;
Neuropterida Whiting & Carpenter & Wheeler & Wheeler, 1977.

Hierarchical name: **Myrmeleon/f1=Hemerobius/g1** (incl. *Raphidia, Chauliodes*) [f: Myrmeleonides Latreille, 1802: 287 (page priority upon Hemerobiini Latreille, 1802: 288; priority by first reviser: Myrmeleonina MacLeay, 1821); g: *Hemerobius* Linnaeus, 1758: 549, type-species *H. humulinus* Linnaeus, 1758 (designated by the Commission, Opinion 211, 1954)].

Typified name in use: **Myrmeleontidea** SENSU Rohdendorf 1977.

NOMENCLATURAL COMMENTS. The name **Neuropteroidea** Handlirsch, 1903 is well known, and the name **Neuropterida** Whiting et al., 1977 is its evident junior circumscriptional synonym. In spite of this, some authors prefer to use Neuropterida instead of Neuropteroidea. Probably they think that the name Neuropteroidea should be rejected, because it contains the suffix with ending "-oidea", which belongs to superfamily, but not to taxa of other ranks (ICZN 29.2) [International Code of Zoological Nomenclature, 1999]. However, this rule can be applied only to typified names of the family-group, but not to other names (ICZN 29.2.1). The name Neuropteroidea does not belong to family-group in any sense (either strict sense of the ICZN, or wide sense formulated by Kluge [1999]), because it is not formed from any generic name; thus, its ending "-oidea" does not contradict ICZN. Unlike Neuropteroidea, another superordinal name from the same Handlirsch's classification — Panorpoidea — really should be rejected, because it is a typified family-group name whose rank is not superfamily.

STATUS OF NEUROPTEROIDEA. While the taxon Neuropteroidea is widely accepted, its autapomorphies are not well known, so some authors regard it to be a plesiomorphon[1].

Some authors regard Neuropteroidea to be paraphyletic, because assume that Meganeuroptera and Coleoptera have a sister relationship. The only reason for this is an assumption that a proximal widening of hind wing, which is characteristic for Meganeuroptera, is a first step toward a hind-motor wing specialization, which is characteristic for Coleoptera [Brodsky, 1994]. How-

1 The term "plesiomorphon" was introduced by Kluge [2004] to indicate a taxon which has no autapomorphies, being possibly paraphyletic, but whose paraphyly (as well as holophyly) is not proven [http://www.bio.pu.ru/win/entomol/KLUGE/plesiomorphon.htm].

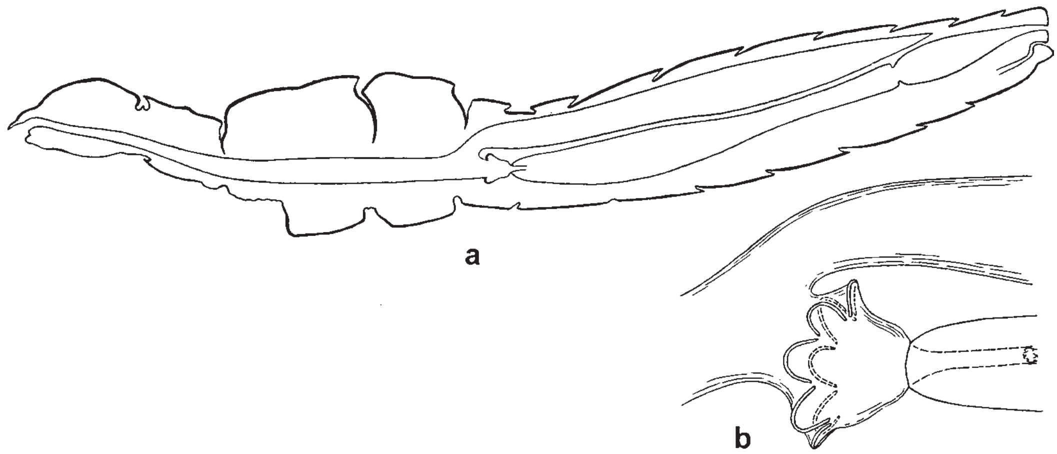


Fig. 1. Imago of *Chrysoperla carnea*: a — longitudinal section with alimentary canal; b — proventriculus and base of dorsal diverticulum.

Рис. 1. Имаго *Chrysoperla carnea*: а — продольный срез с пищеварительным каналом; б — провентрикулюс и основание дорсального дивертикула.

ever, the same hind wing widening occurs in *Ithone*, which belongs to Birostrata.

Another idea about paraphyly of Neuropteroidea is connected with an assumed synapomorphy of all Metabola except for Meganeuroptera. Sehnal [1985] reported: "To stress the similarity between larvae, pupae and adults of Megaloptera, this order and occasionally also Raphidioptera were by some authors separated from other endopterygotes (called Euholometabola) as Eoholometabola". Like F. Sehnal, I was failure to find the original paper where the taxa names Euholometabola and Eoholometabola were proposed. Meganeuroptera really have an outstanding type of larval/pupal transformation, where the phase of leg diminishing is absent, and some of leg muscles are retained, while Rhaphidioptera in this respect are similar to Birostrata and other Metabola; however, some facts indicate that metamorphosis of Meganeuroptera is a result of secondary simplification, but not a plesiomorphy [Kluge, in press].

Most probably, Neuropteroidea is a holophyletic taxon, as it has the following autapomorphies.

AUTAPOMORPHIES OF NEUROPTEROIDEA.

• Imago (but not larva) has a peculiar dorsal diverticulum of stomodaeum [Grinfeld, 1962]. This diverticulum arises from dorsal wall at hind part of foregut just before proventriculus, is directed backward and lies above midgut (Fig. 1a). Proventriculus has a peculiar structure: it is armed by 8 arched sclerites which form a flower-like figure directed by its petals anteriorly (Fig. 1b). This proventricular armature is found in *Raphidia*, *Chrysoperla*, *Osmylus* and *Mantispa*; but not found in *Sialis* and *Sisyra*.

• On fore wing, fore margin is convex in proximal part so that costal field is widened in this area, gradually narrowing toward apex; the costal field has many oblique cross-veins; Sc goes parallel to RA up to wing apex, where it arches backward together with RA (or fused with RA), repeating shape of fore margin of the wing. RS usually has pectinate branching.

In many representatives some of this characters are lost: in most myrmeleontids wings are narrowed, so the widening of costal field is not expressed; in Rhaphidioptera and Dictyneuroptera Crampton 1916 (= Mantispa/fg1) distal parts of Sc is transformed to a pterostigma, so Sc looks falling into the fore margin of wing before the pterostigma; Rhaphidioptera, Sialis/fg1 and some Birostrata have a small number of RS branches, so its pectinate branching is non-expressed. In Coniopteryx/fg1 all these characters of wing venation are lost.

• Ovipositor lost gonapophyses of the 9th abdominal segment (which initially for Amyocerata couple with gonapophyses of 8th segment to form the working part of ovipositor); working part of ovipositor is constituted by coxites of the 9th abdominal segment, which are fused dorsally, filled with intrinsic muscles (new formations), largely desclerotized and bear a pair of longitudinal lateral sclerites articulated with lateral sides of the 9th abdominal tergite. If the ovipositor is long (in Rhaphidioptera, Dilar/fg1 and Dictyneuroptera–Trichoscelia/fg1) it is actively flexible and in rest arched dorsally. In most representatives ovipositor is short or reduced.

• In imago the 10th abdominal tergite bears a pair of groups of trichobothria. In some taxa they are lost [Aspöck et al., 2001].

• In larva a pair of lateral cervical sclerites are fused ventrally to form an integral unpaired semicircular sclerite (Fig. 15). Imaginal cervical sclerites either retain the plesiomorphic paired structure, or have the larval structure (in Eumegaloptera–Corydalus/f3=g1), or have a modification of their own (in Rhaphidioptera).

MOUTH APPARATUS. Imaginal maxilla has setose lacinia (Fig. 16) and probably is initially specialized for pallinophagy (while Rhaphidioptera and some Birostrata are carnivorous, and Meganeuroptera and some Birostrata are aphagous). Other features of imaginal mouth apparatus are either evidently plesiomorphic, or variable. In all Neuropteroidea maxilla has structure close to the initial for Hexapoda (see above), with

distinctly developed cardo, stipes, galea, lacinia and 5-segmented palp. Imaginal mandible is biting, either functional, or non-functional.

Structure of larval mouth apparatus is quite different in Birostrata, Rhaphidioptera, Sialis/fg1 and Eumegaloptera (see below).

CLASSIFICATION. Traditionally, Neuropteroidea are divided into three subordinate taxa — Birostrata, Rhaphidioptera and Meganeuroptera. Some authors do not recognize the taxon Meganeuroptera and accept four directly subordinate taxa — Birostrata, Rhaphidioptera, Sialis/fg1 and Eumegaloptera (see below).

1.1. **Birostrata**

Circumscriptional names:
Euneuropteroidea Krausse & Wolff, 1919 (see comments);
Birostrata Kluge, **taxon nov.**

In circumscription also matches: **Megaloptera** SENSU Burmeister, 1839 (non Latreille, 1802, nec 1807); **Neuroptera** SENSU Handlirsch, 1903 (non Linnaeus, 1758); **Stegoptera** SENSU Banks, 1907 (non Dumeril, 1806); **Planipennia** SENSU Heymons, 1915 (non Planipennes Latreille, 1817, nec Planipennia Burmeister, 1839).

Hierarchical name: **Myrmeleon/f2=Hemerobius/g2** (sine *Raphidia, Chauliodes*; incl. *Chrysopa*, *Osmylus*, *Sisyra*, *Coniopteryx*, *Dilar*, *Mantispa*, *Berotha*, *Ithone*, *Polystoechotes*, *Nevrorthus*).

Typified names in use: **Myrmeleonina**, **Myrmeleontida**, **Hemerobiina**, **Hemerobiites**, **Hemerobida**, **Hemerobidae**, **Hemerobiida**, **Hemerobiidae**, **Hemerobiidi**, **Hemerobiiformes**, **Hemerobiodea**.

NOMENCLATURAL COMMENTS. Nowadays this taxon is often called either Neuroptera or Planipennia, but neither name in its original circumscription match this taxon.

The name **Neuroptera** Linnaeus, 1758 was originally applied to an order which united genera *Libellula* (matching Odonata), *Ephemera* (matching Ephemeroptera), *Phryganea* (matching Trichoptera + Plecoptera + part of Meganeuroptera), *Hemerobius* (matching Birostrata + part of Meganeuroptera + Isoptera + Copeognatha), *Panorpa* (matching Mecaptera) and *Raphidia* (matching Rhaphidioptera). Now Neuroptera SENSU Linnaeus, 1758 is regarded to be a paraphyletic taxon ancestral to other orders of winged insects in the Linnaean classification. Subsequently, the paraphyletic order Neuroptera was broken down to a number of smaller natural orders, one of which was given the name Neuroptera. MacLeay [1821] designated the genus *Libellula* as the type for the name Neuroptera, so some workers splitting Linnaean Neuroptera into smaller orders applied the name Neuroptera to an order including odonates (*Libellula*). Others, however, used, and still do, the name Neuroptera to refer to orders of various circumscriptions not including *Libellula*.

The name **Planipennes** Latreille, 1817 is often spelled out as "Planipennia", because some people mistake "Planipennes" for a French spelling; however, elsewhere Latreille [1825] spells "Planipennes" both in Latin and French. Originally [Latreille, 1817] the family Planipennes matched in circumscription Plecoptera + Isoptera + Copeognatha + Birostrata + Meganeuroptera + Rhaphidioptera + Mecaptera. Planipennes is a junior circumscriptional synonym of **Stegoptera** Dumeril, 1806. Burmeister [1839] was the first to use the spelling "Planipennia". The taxon **Planipennia** Burmeister, 1839 matches in circumscription Birostrata + Meganeuroptera + Rhaphidioptera + Mecaptera.

The only name whose original circumscription possibly matches the taxon under consideration is **Euneuropteroidea** Krausse & Wolff, 1919. In our paper, where this name is discussed [Kluge & Krivokhatsky, 1998] an error takes place; there is written: "The taxon Euneuropteroidea was proposed as a volumetrical taxon, but not as a ranking one (for explanation — see above). It means, that in further classifications the name Euneuropteroidea should be used for taxa of the same allowed volume (i.e. including at least type species of all families listed above as included, and excluding at least the taxa of Neuropteroidea listed above as excluded ones) ...". This wrong sentence came from the previous version of the text, where we proposed a new name for this taxon, and unfortunately was not corrected. The correct text should be: "In further classifications the name Euneuropteroidea should be used for taxa of the same allowed volume (i.e. including at least type species of all orders listed in Krausse & Wolff [1919] as included, and excluding all taxa listed in the same paper as excluded ones) ...". The ordinal names listed by Krausse & Wolff [1919] as belonging to Euneuropteroidea, are Myrmeleonida, Ascalaphida, Nemopteridida (misprint "Neuropteridida"), Sisyrida, Osmylida, Kalligrammida, Nymphitida, Mesochrysopida, Prohemerobiida, Solenoptilida, Dilarida, Polystoechotidida, Nymphesida, Hemerobiida, Chrysopida, Mantispida and Coniopterygida.

Thus, among the taxa originally included into Euneuropteroidea, there are extinct taxa Prohemerobius/fg, Solenoptilon/fg, Kalligramma/fg, Nymphites/fg and Mesochrysopa/fg, known only as fossil adults. The only reason to unite these taxa with Birostrata, is that their wing venation have features of Neuropteroidea (see above), but have no special features of Rhaphidioptera, Sialis/fg1 or Eumegaloptera; at the same time, no one of these taxa has distinct diagnosis basing on wing venation. Probably, the taxon Euneuropteroidea is poorly a plesiomorphon, ancestral for Rhaphidioptera and Meganeuroptera and existing since Permian (or at least since Lias, from which the type-species of *Prohemerobius* Handlirsch, 1906 was described).

Unlike Euneuropteroidea, the taxon **Birostrata**, taxon nov. is holophyletic and characterized by an autapomorphy in larval structure (see below); its original listed membership includes only Myrmeleon/fg, Hemerobius/fg, Chrysopa/fg, Osmylus/fg, Sisyra/fg, Coniopteryx/fg, Dilar/fg, Mantispa/fg, Berotha/fg, Ithone/fg, Polystoechotes/fg and Nevrorthus/fg — taxa, for all of which this apomorphy is known. If necessary, one can use the name Birostrata as "**Neuroptera-Birostrata**", because all representatives of Birostrata were originally includ-

ed into the artificial order Neuroptera Linnaeus, 1758. Unlike Euneuropteroidea, which are reported from Permian and Lias, the taxon Birostrata possibly is no older than Late Jurassic.

AUTAPOMORPHY OF BIROSTRATA. The only known autapomorphy of Birostrata is a unique paired sucking-piercing mouth apparatus of larva, which invariably exists in all representatives (with this the name "Birostrata" is connected).

LARVAL MOUTH APPARATUS. Besides labrum and labium with labial palps, mouth apparatus includes a pair of unusual piercing-sucking stylets composed by a pair of modified mandibles and a pair of modified distal portions of maxillae. These movable distal portions of maxillae have complex origin, and I suggest to call them **maxillary malae**. The mandible and the maxillary mala of each side are coupled together by a peculiar lock [Gaumont, 1976] and function as an integral movable stylet. Homology of the maxillary malae was the subject of discussion and is clarified now (see below).

MAXILLARY COMPONENT OF STYLET. Maxilla of larval Birostrata consists of a basal portion and a distal portion. The basal portion is formed by two sclerites (often called cardo and "stipes"), which constitute a part of ventral wall of the head. The distal portion (maxillary mala) is a movably articulated process directed anteriorly; it couples with mandible and constitutes a ventral half of the piercing-sucking stylet. Maxilla has the following musculature (Fig. 2) [Rousett, 1966]: (1) intrinsic muscles inside proximal part of the maxillary mala (dilators of sucking channel); (2) muscle(s) going from base of the mala into the "stipes" (present not in all representatives); (3) strong muscle(s) going from base of the mala to cranial wall; (4) muscle(s) going from base of the mala to tentorium; (5) muscle(s) going from the "stipes" to tentorium; (6) muscle(s) going from the cardo to tentorium. Unlike imago and pupa (Fig. 3), larva has no muscle going from the cardo to cranium.

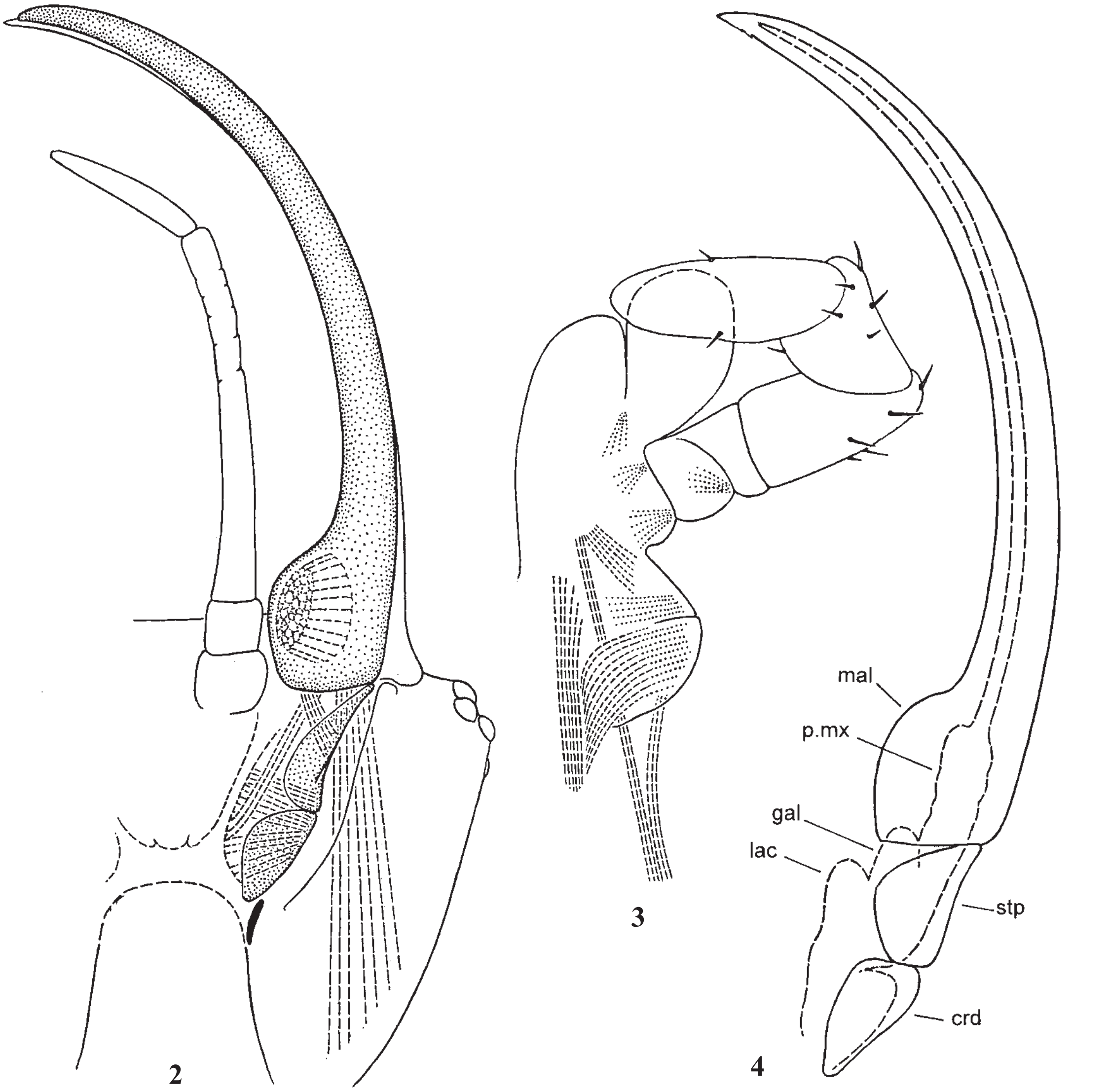
Basing on musculature, Rousett [1966] discussed all possible hypotheses about origin of these parts of maxilla. Hypothesis 1: maxillary mala is either lacinia, or galea; the basal portion of maxilla consists of the whole stipes and the cardo. Hypothesis 2a: maxillary mala includes the whole stipes (possibly with lacinia, galea and palp); the basal portion of maxilla represents only the cardo divided into two pieces. Hypothesis 2b: maxillary mala includes a part of stipes (possibly with lacinia, galea and palp); the basal portion of maxilla consists of the rest part of stipes and the cardo. Presence of the muscle going from mala to tentorium excludes the Hypothesis 1, because only stipes and cardo (but not lacinia, galea or palp) have muscles going to tentorium. Presence of the muscle going from mala to stipes (i.e. to the distal sclerite of basal portion of maxilla) excludes the Hypothesis 2a, because only stipes (but not cardo) has muscles going to lacinia, galea and palp. Presence of the muscle going from mala to cranium excludes assumptions that mala is the galea or the palp, because only lacinia and cardo have muscles going to cranium. Thus, base of mala includes at least lacinia and a distal portion of stipes movably articulated with the proximal portion of stipes, which retains its normal position, structure and function.

The Rousett's conclusion, based on musculature, is correct. A question, which was not answered, is which maxillary parts attached to stipes and lacinial base (lacinia, galea, or palp) constitute the long piercing-sucking portion of the maxillary mala, and which are reduced.

I examined larval/pupal transformation in representatives of two species of Chrysopidae and one species of Myrmeleontidae. Larvae of *Chrysoperla carnea* (Stephens, 1836 [*Chrysopa*]) were collected in July 2004 in Borisovka of Belgorod Province (Russia), and kept in cages; 8 pronymphs taken from cocoons were fixed at various phases of development. One pronymph of *Chrysotropia ciliata* (Wesmael, 1841 [*Chrysopa*]) was got from larva collected in August 2004 in Saint-Petersburg (Russia). Larvae of *Myrmeleon bore* (Tjeder, 1941 [*Grocus*]) were collected in August 2004 on southern shore of Gulf of Finland in Izhora near Saint-Petersburg and kept in cages; 25 pronymphs were fixed at various phases of development. All pronymphs were dissected and mounted on slides in Canadian balsam.

The examined species of Chrysopidae have such a phase of pronymphal development, when musculature of mouthparts is already lost, hypoderm of mouthparts is strongly diminished and starts to get the pupal shape, but retains slender stretched tips, which are still inserted into the larval cuticular appendages (Figs 4, 6, 11, 12). This phase corresponds to the arbitrary 2nd and 3rd phases of leg transformation, when the hypodermal parts of legs also retain vestigial apical processes [Kluge, in press: Figs 33a–b, 34, 38, 41]. Presence of the stretched vestigial tips of future pupal appendages inserted into the larval cuticular appendages allows to understand homology between larval and pupal appendages (but not homology between their segments, because at least in legs ontogenetic homology of segments is broken). The examined species of *Myrmeleon* has no such phase of development; when its mouthparts transform from larval to pupal, their tissues at first degenerate and move out from the corresponding larval cuticle, and only after this get pupal shape. So conclusions about homology of maxillary parts are based mainly on development of Chrysopidae.

Among the examined pronymphs of Chrysopidae, 4 specimens of *Chrysoperla carnea* and one specimen of *Chrysotropia ciliata* are at the phase when appendages retain hypodermal projections inserted into the larval cuticular appendages. In all these specimens hypoderm of the future pupal maxilla already has distinguishable lacinia, galea and palp, and tip of the palp continues to a slender process which is inserted into the larval cuticular stylet-like distal portion of maxillary mala (Figs 4, 6, 11, 12). At the same time, the future pupal galea locates inside the proximal swollen part of the larval cuticular maxillary mala, and the future pupal lacinia

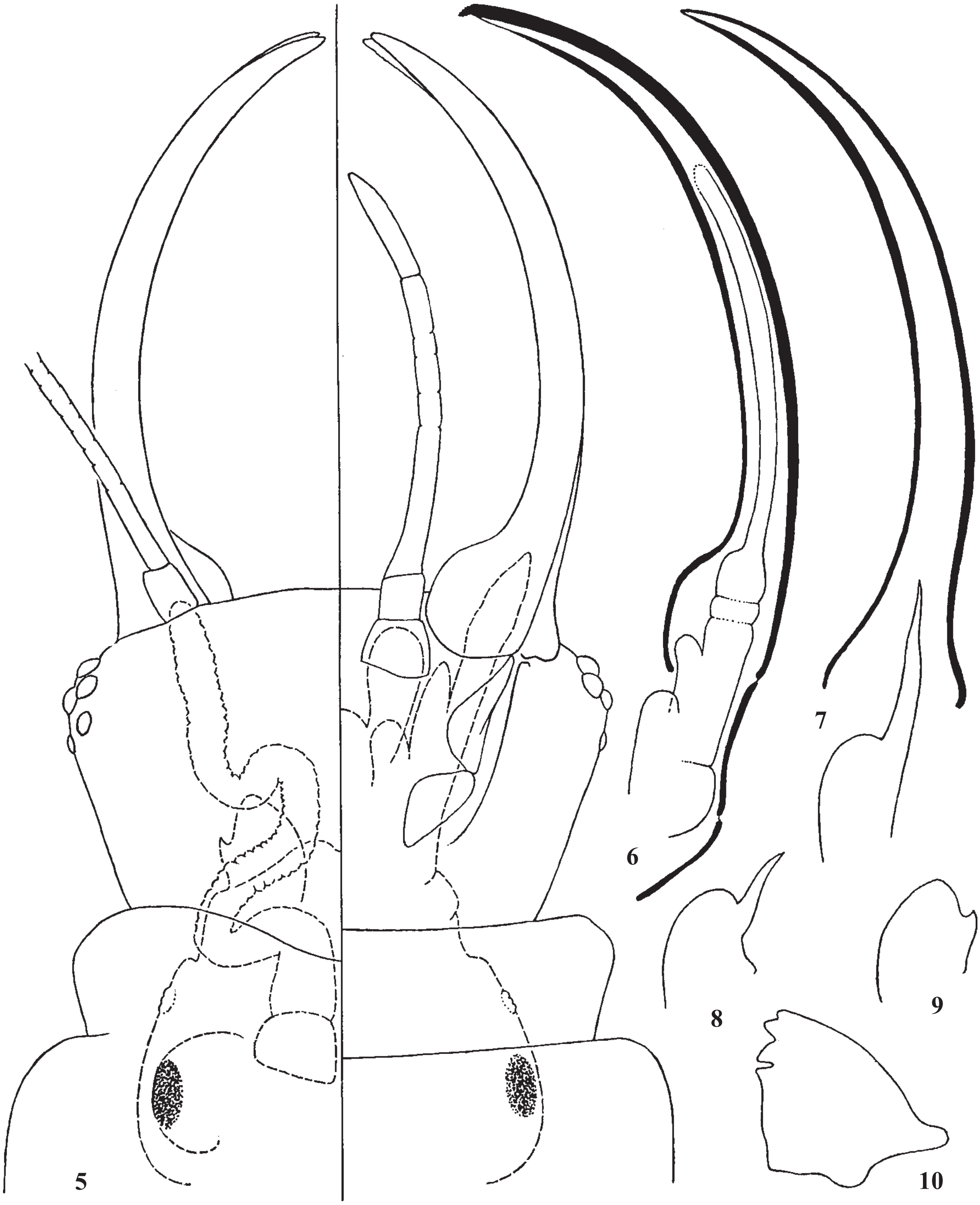


Figs 2–4. Maxilla of *Chrysoperla carnea*, ventral view: 2 — left half of head of active larva (only maxillary sclerites dotted; tentorium and maxillary muscles shown by interrupted lines; other muscles not drawn); 3 — maxilla of pupa (anlages of pupal-imaginal muscles shown by interrupted and dotted lines); 4 — maxilla of pronymph at that phase, when under larval cuticle (shown by integral line) hypoderm is detached and starts to get pupal shape (shown by interrupted line). Abbreviations: crd — larval cardo; gal — future pupal galea; lac — future pupal lacinia; mal — larval maxillary mala (distal portion of stipes + lacinia + galea + palp); p.mx — future pupal maxillary palp; stp — larval proximal portion of stipes.

Рис. 2–4. Максилла *Chrysoperla carnea*, вентрально: 2 — левая половина головы активной личинки (только максиллярные склериты пунктированы; тенториум и максиллярные мышцы показаны прерывистыми линиями; другие мышцы не нарисованы); 3 — максилла куколки (зачатки куколочно-имагинальных мышц показаны прерывистыми и пунктирными линиями); 4 — максилла пронимфы на той фазе, когда под личиночной кутикулой (показанной сплошной линией) гиподерма отслоилась и начинает приобретать куколочную форму (показана прерывистой линией). Сокращения: crd — личиночное кардо; gal — будущая куколочная галеа; lac — будущая куколочная лациния; mal — личиночная максиллярная мала (дистальная часть стипеса + лациния + галеа + щупик); p.mx — будущий куколочный максиллярный щупик; stp — личиночная проксимальная часть стипеса.

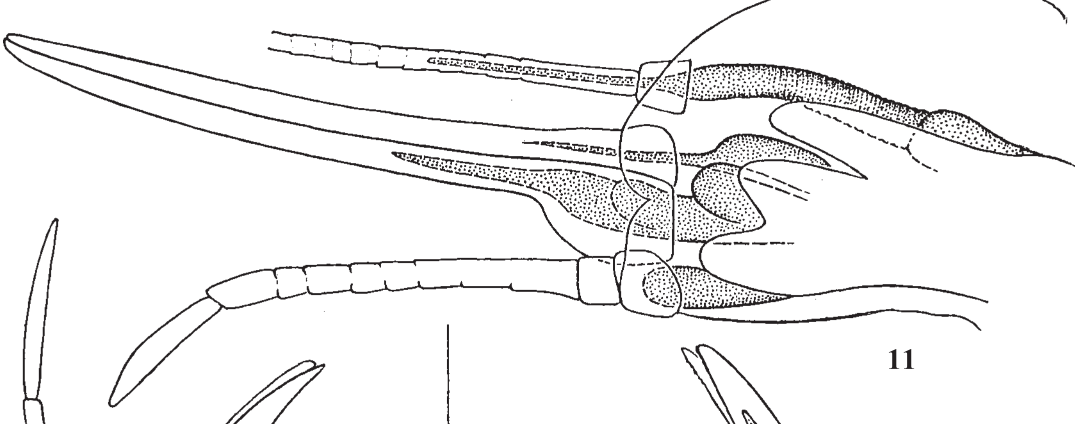
locates more proximally. In some specimens boundaries between segments 3, 4 and 5 of the future pupal maxillary palp are already visible (Fig. 6). Among the examined pronymphs of *Myrmeleon bore*, about 8 specimens have more or less distinguishable lacinia, galea and palp of the future pupal maxilla, and at the same time retain some connection between it and the larval cuticular maxillary mala; in all of them only the future pupal maxillary palp is connected with, or partly inserted into the larval cuticular mala (in other specimens fixed at the same phases of development, parts of the future pupal maxilla are non-distinguishable).

Such development of pupal maxilla allows to conclude that in larva of Birostrata maxillary palp has not been reduced, but gave rise to the long, heavily sclerotized, pointed, non-segmented, stylet-like, distal portion of maxillary mala; galea, lacinia and apical portion of stipes are completely fused with base of the palp.

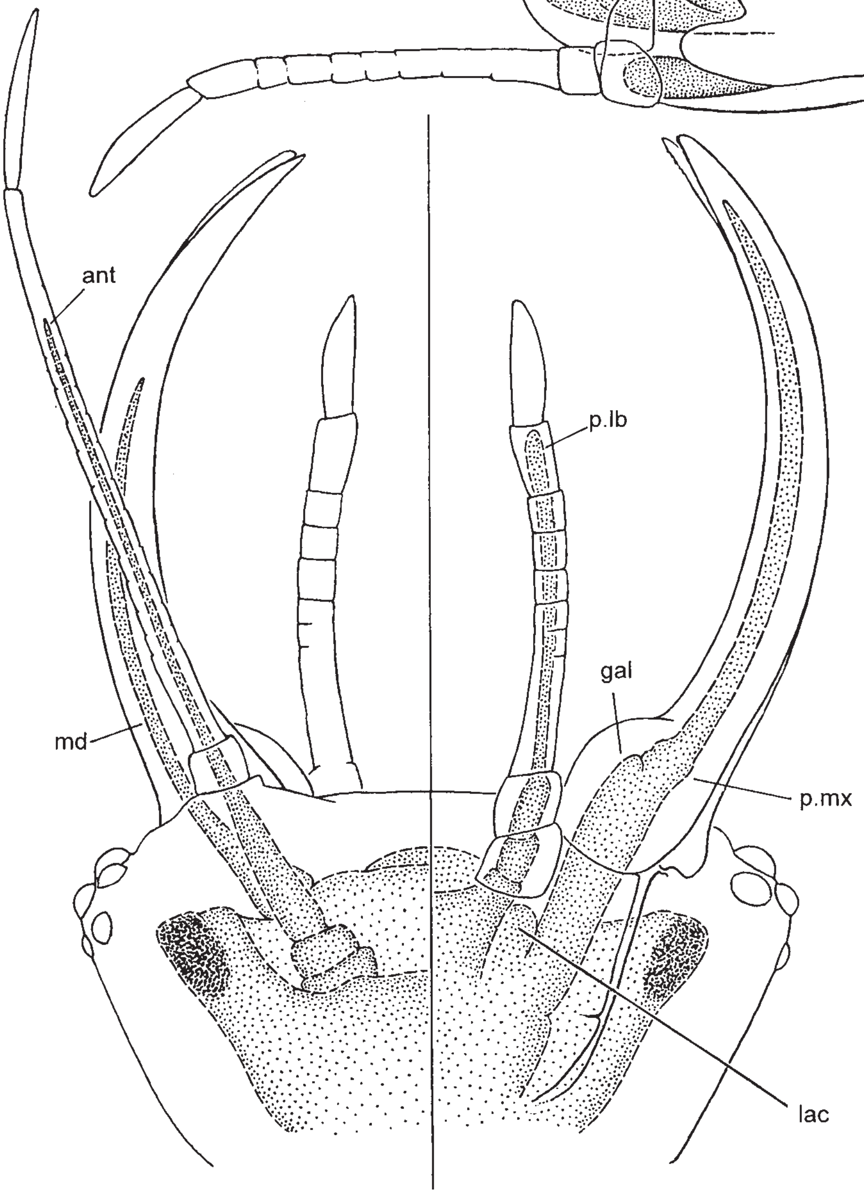


Figs 5–10. Head of *Chrysoperla carnea*: 5–9 — pronymphs: 5 — head of pronymph (in left — dorsal view; in right — ventral view; integral lines — larval cuticle; interrupted lines — hypoderm getting shape of future pupal head and appendages; imaginal eyes dotted); 6 — optic section of maxilla (black filled — optic section of larval cuticle; thin line — outline of hypoderm getting shape of future pupal maxilla); 7 — optic section of mandible (black filled — optic section of larval cuticle; thin line — outline of hypoderm getting shape of future pupal mandible); 8 — hypoderm getting shape of future pupal mandible at next phase of pronymphal development; 9 — the same, at next phase (the same specimen as in Fig. 5); 10 — mandible of pupa.

Рис. 5–10. Голова *Chrysoperla carnea*: 5–9 — пронимфы: 5 — голова пронимфы (слева — дорсально; справа — вентрально; сплошные линии — личиночная кутикула; прерывистые линии — гиподерма, приобретающая форму будущей куколочной головы и ее придатков; имагинальные глаза пунктированы); 6 — оптический срез максиллы (черная заливка — оптический срез личиночной кутикулы; тонкие линии — очертания гиподермы, приобретающей форму будущей куколочной максиллы); 7 — оптический срез мандибулы (черная заливка — оптический срез личиночной кутикулы; тонкие линии — очертания гиподермы, приобретающей форму будущей куколочной мандибулы); 8 — гиподерма, приобретающая форму будущей куколочной мандибулы в следующей фазе пронимфального развития; 9 — то же, в следующей фазе (тот же экземпляр, что на рис. 5); 10 — мандибула куколки.



11



12

Figs 11–12. Chrysopidae, head of pronymph: 11 — *Chrysoperla carnea*, left half of head, view from median section; 12 — *Chrysotropia ciliata*, head (in left — dorsal view; in right — ventral view). Larval cuticle shown as colourless; surface of hypoderm (which gets shape of future pupal parts) dotted, hidden parts of hypoderm shown by interrupted line. Abbreviations: ant — future pupal antenna; gal — future pupal galea; lac — future pupal lacinia; md — future pupal mandible; p.lb — future pupal labial palp; p.mx — future pupal maxillary palp.

Рис. 11–12. Chrysopidae, голова пронимфы: 11 — *Chrysoperla carnea*, левая половина головы, вид с медиального среза; 12 — *Chrysotropia ciliata*, голова (слева — дорсально; справа — вентрально). Личиночная кутикула показана как бесцветная; поверхность гиподермы пунктирована, скрытые части гиподермы показаны прерывистой линией. Сокращения: ant — будущая куколочная антенна; gal — будущая куколочная галеа; lac — будущая куколочная лациния; md — будущая куколочная мандибула; p.lb — будущий куколочный лабиальный щупик; p.mx — будущий куколочный максиллярный щупик.

MANDIBULAR COMPONENT OF STYLET. The mandibular component of larval piercing-sucking stylet undoubtedly represents the whole mandible: it has a usual for Metapterygota articulation with head capsule and strong muscles going from its base to cranium.

Pupal and imaginal mandible of Birostrata has a distinct pointed apical incisor and a medial biting edge formed by fused kinetodontium and mola (this edge can be smooth or dentate, but has kinetodontium and mola indistinguishable). Pupal mandibles are functional; in course of larval/pupal transformation in pronymphal phase, all larval mandibular musculature at first completely disappears, and than new pupal-imaginal mandibular musculature appears.

When muscle-less primordium of pupal mandible develops inside the larval cuticular mandible of pronymph (at the same phase, as maxilla — see above) its incisor develops not from the point of larval mandible, but as a blunt outgrow of its median side; slender pointed process, which is a remainder of the larval mandibular stylet, locates on lateral side of the future pupal mandible (Fig 7). During subsequent development, this process becomes shorter and shorter (Figs 8, 9), and finally disappears (Fig. 10).

Such development allows to conclude that the larval mandibular portion of piercing stylet proceeds not from the incisor, but from a peculiar lateral outgrow of mandible. The lateral mandibular outgrowth of larval Birostrata resembles mandibular task of certain larval Ephemeroptera [Kluge, 2004].

ASSUMED HOMOLOGY. Possibly, the mandibular and the maxillary components of stylet originated from serially homologous parts of mandible and maxilla — their telopodites. Maxillary telopodite is a maxillary palp; in most Hexapoda (including pupa and imago of Birostrata) it is distinctly developed and 5-segmented. Mandibular telopodite was lost in the common ancestor of Hexapoda or earlier, in the common ancestor of Atelocerata [Kluge, 2000]. However, it is not excluded that the place on mandible where the mandibular telopodite was lost, retains ability to produce a non-segmented process. Such process could independently appear in some non-related taxa of Ephemeroptera-Furcatergaliae, in larval Birostrata and possibly in some other insects.

1.2. **Rhaphidioptera**

Circumscriptional names:

Tetramera Billberg, 1820 (non Tertamera Dumeril, 1806);
Aponeuroptera Crampton, 1916;
Rhaphidioptera Navas, 1916;
Raphidioptera Martynov, 1938.

Hierarchical name: **Raphidia/fg1** (incl. *Inocellia*) [f: Raphidinae Latreille, 1810; g: *Raphidia* Linnaeus, 1758; type-species *R. ophiopsis* Linnaeus, 1758].

Typified names in use: ***Raphidia***, **Raphidiacea**, **Raphidiades**, **Raphididae**, **Raphidides**, **Raphidiidae**, **Raphidiidea**, **Raphidiina**, **Raphidiides**, **Raphidina**, **Raphidinae**, **Raphidiodea**, **Raphidioidea**, **Raphidites**.

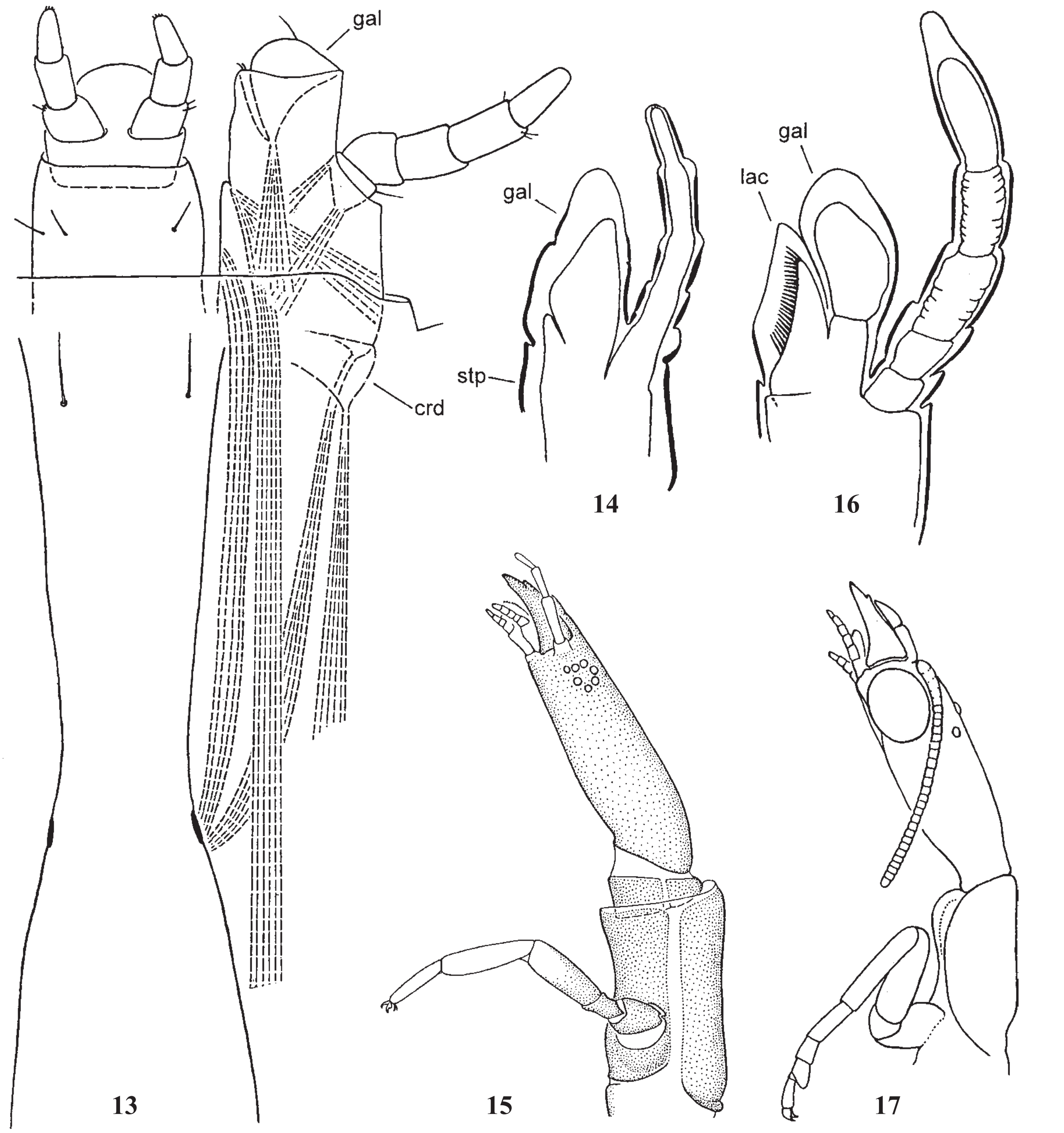
NOMENCLATURAL COMMENTS. Basing on traditions of transliteration from Greek to Latin, Navás [1916] decided that the correct spelling of the generic name was not *Raphidia*, but *Rhaphidia*; because of this, he used the family name Rhaphididae and created the new ordinal name Rhaphidioptera. According the rules of the actual International Code of Zoological Nomenclature [1999], generic name should be used in its original spelling independently if it corresponds to grammatical rules or not (ICZN 32.5.1); subsequent spelling different from the original, i.e. an unjustified emendation, is regarded to be a junior objective synonym, with its own author and date (ICZN 33.2.3); family-group name should be formed from the original spelling of generic name (ICZN 35.4.1). Because of this, the generic name should be *Raphidia* Linnaeus, 1758, but not *Rhaphidia* Billberg, 1820; family-group names should be formed from *Raphidia*, but not from *Rhaphidia*. However, these rules can not be spread to the name Rhaphidioptera: this name does not belong to the family-group, because it is formed not from generic name, suffix and ending only, but includes also a base "-pter-". Unlike typified names (i.e. family-group names in widest sense) the name **Rhaphidioptera** Navas, 1916 should be used in its original spelling with its own author and date, and the name **Raphidioptera** Martynov, 1938 should be regarded as an unjustified emendation, i.e. junior objective synonym, and used with its own author and date.

AUTAPOMORPHIES OF RHAPHIDIOPTERA. This is a small group of insects with rather uniform structure, so it has many autapomorphies [Aspöck & Aspöck, 2004]. One of autapomorphies is elongate, prognathous head with long gula, so bases of all mouthparts are translocated to the extreme anterior margin of the head.

MOUTH APPARATUS. In all stages of development (larva, pupa and imago) head has the same structure (Figs. 13, 15, 17): it is sharply prognathous, elongate, with long gula; tentorium is vestigial, and posterior tentorial pits locate at the middle of the long sclerotized ventral side of the head far from mouthparts and far from occipit. Maxillae and labium are located anteriorly; their bases are hidden by anterior margin of the gula (Fig. 13). Muscles going from maxillae and labium to cranium and tentorium (cardinal-cranial, cardinal-tentorial, stipital-tentorial, lacinial-cranial and labial-tentorial muscles) are strongly elongated, longitudinal, nearly parallel and can somewhat retract the maxillae and the labium into the head (Fig. 13). These muscles are equally developed in larva, pupa and imago and seem to retain without lysis during metamorphosis.

MAXILLA. Unlike the maxilla initial for Hexapoda, larval and imaginal maxilla of Rhaphidioptera has stipes cylindrically projected, with developed median sclerotized wall proximad of lacinia (Fig. 14: stp), so the lacinial-cranial muscle passes trough the stipes (Fig. 13) (such structure is not found in other Neuropteroidea). At all stages, maxillary palp is 5-segmented and attached on lateral side of the stipes.

Larval maxilla has no separate lacinia; galea is retractable and locates on apex of cylindrical stipes (Figs 13, 14). Imaginal maxilla has well-separated lacinia (se-



Figs 13–17. *Raphidia* spp.: 13–15 — larva: 13 — part of head of active larva, ventral view; galea partly retracted into stipes, cardo and base of stipes retracted into head (maxillary muscles and hidden parts of maxilla shown by interrupted lines; other muscles not drawn); 14 — optic section of pronymphal maxilla (black filled — optic section of larval cuticle; thin line — outline of hypoderm getting shape of future pupal maxilla); 15 — larval head and prothorax, lateral view; 16–17 — pupa: 16 — optic section of maxilla (black filled — optic section of pupal cuticle; thin line — outline of imaginal maxilla developing inside); 17 — pupal head and prothorax, lateral view. Abbreviations: crd — cardo; gal — galea; lac — lacinia; stp — median wall of stipes.

Рис. 13–17. *Raphidia* spp.: 13–15 — личинка: 13 — часть головы активной личинки, вентрально; галеа частично втянута в стипес, кардо и основание стипеса втянуты в голову (максиллярные мышцы и скрытые части максиллы показаны прерывистыми линиями; другие мышцы не нарисованы); 14 — оптический срез пронимфальной максиллы (черная заливка — оптический срез личиночной кутикулы; тонкая линия — очертания гиподермы, приобретающей форму будущей куколочной максиллы); 15 — личиночная голова и переднегрудь, латерально; 16–17 — куколка: 16 — оптический срез максиллы (черная заливка — оптический срез куколочной кутикулы; тонкая линия — очертания имагинальной максиллы, развивающейся внутри); 17 — куколочная голова и переднегрудь, латерально. Сокращения: crd — кардо; gal — галеа; lac — лациния; stp — медиальная стенка стипеса.

tose, as in other Neuropteroidea); galea is non-retractable (Fig. 16). During the larval/pupal and pupal/imaginal transformations imaginal lacinia develops from a median-distal part of the integral larval stipes, which actually represents a result of fusion of stipes and lacinia (Figs 14, 15).

MANDIBLE. Pupal mandibles are functional; probably, mandibles retain functional musculature during all metamorphosis (unlike Birostrata). At pronymphal phase, the future pupal mandible locates inside the larval cuticular mandible in such a way, that apex of the

pupal incisor lies inside apex of the larval incisor (as in Fig. 21) (unlike Birostrata, whose apices of larval and pupal mandibles are different — see above).

1.3. **Meganeuroptera**

Circumscriptional names:
Semblides Latreille, 1825 (non Semblis/fg);
Meganeuroptera Crampton, 1916;
Eumegalopterida Krausse & Wolff, 1919.

In circumscription also matches: **Megaloptera** SENSU Latreille, 1807 (non 1802).

Hierarchical name: **Corydalus/f1=Chauliodes/g1** (incl. *Sialis*) [f: Corydalides, Leach 1815; g: *Chauliodes* Latreille, 1796, type-species *Hemerobius pectinicornis* Linnaeus, 1763 (designated by Latreille, 1802 & 1810)].

Typified names in use: **Corydalides**, **Corydalida**.

NOMENCLATURAL COMMENTS. The oldest correct circumscriptional name of the taxon under consideration is **Meganeuroptera** Crampton, 1916. The name Meganeuroptera Crampton, 1916 (formed as "mega" + "Neuroptera") should not be confused with its junior homonym Meganeuroptera Tillyard, 1918 (formed as "*Meganeura*" + "ptera").

Usually this taxon is called Megaloptera; however, in modern literature the name **Megaloptera** is used in two different senses: for the taxon uniting Rhaphidioptera + Meganeuroptera [Hennig, 1953; Hinton, 1981] or for Meganeuroptera without Rhaphidioptera [Hennig, 1969 and others]. In the past the name Megaloptera was used also in a quite different sense — for Birostrata, i.e. for the taxon which does not include neither Rhaphidioptera, nor Meganeuroptera [Burmeister, 1839 and others]. Originally, the name Megaloptera was introduced by Latreille; in the original publication [Latreille, 1802–1805] this name was used for the taxon uniting genera *Chauliodes*, *Corydalus*, *Sialis* and *Raphidia* — i.e. for Rhaphidioptera + Meganeuroptera. In his next publications [Latreille, 1806–1809 et al.] this author used the name Megaloptera for Meganeuroptera only. Thus, the formal original circumscription of the name Megaloptera Latreille 1802 is Rhaphidioptera + Meganeuroptera. In order to avoid confusion, it is better not to use the name Megaloptera, and if accept the taxon uniting Rhaphidioptera + Meganeuroptera, use for it the junior circumscriptional synonym **Emmenognatha** Borner, 1904.

STATUS OF MEGANEUROPTERA. Some authors do not recognize this taxon and regard Sialis/fg1 to be a sister group to Rhaphidioptera, but not to Eumegaloptera [Štys & Bilinski, 1990]. This conclusion is based on the fact that examined species of *Sialis* and Rhaphidioptera have telotrophic ovaria of a peculiar structure, while examined species of Eumegaloptera have panoistic ovaria [Büning, 1996].

There are only a few non-unique derived characters, which can be regarded as autapomorphies of Meganeuroptera: larvae are aquatic; larval abdomen bears paired lateral gill appendages (whose structure differs in Sialis/fg1 and Eumegaloptera); wings have setae on membrane.

Meganeuroptera are divided into Sialis/fg1 and Eumegaloptera.

1.3.1. **Sialis/fg1**

Hierarchical name: **Sialis/fg1** [f: Sialida Leach, 1815; g: *Sialis* Latreille, 1802, type-species *Hemerobius lutarius* Linnaeus, 1758].

Typified names in use: ***Sialis***, **Sialida**, **Sialidae**, **Sialinae**, **Sialoidea**.

AUTAPOMORPHIES OF SIALIS/FG1. Known representatives of this taxon have rather uniform structure, so the taxon has many autapomorphies. Larva has segmentation on the abdominal gill appendages and a unique ventral tail on the 10th abdominal segment.

MOUTH APPARATUS. In most respects mouth apparatus of larva, pupa and imago is similar and close to ancestral for Hexapoda; only larval maxillae have significant difference from the pupal-imaginal ones.

MAXILLA. In larva galea and palp arise from a common basal segment, and palp looks as 4-segmented (Fig. 18). In pupa (Fig. 20) and imago labial palp is separate from galea and distinctly 5-segmented. Röber [1941] wrongly described musculature of larval maxilla and confused lacinia with galea.

Larvae of *Sialis sordida* Klingstedt, 1932 ready to pupation were collected 11 May 2004 at the bank of Peterhoff Canal (Saint-Petersburg, Russia) in the upper layer of ground and in rotten wood. Their development continued in laboratory. 12 specimens were fixed at, or near, the moment of larval/pupal ecdysis — 5 larvae ready to moult, 4 moulting specimens and 3 pupae just after moult. They were dissected and mounted on slides in Canadian balsam.

Homology between parts of larval and pupal maxillae can be clarified (1) by comparison of musculature, (2) by comparison of setation and (3) by examination of development of pupal tissues inside larval cuticle.

(1) Maxillary musculature is identical in larva, pupa and imago, and only partly degenerates during larval/pupal transformation. Labial palp has only one intrinsic muscle in the 1st segment; other maxillary musculature is typical for Hexapoda. The cardinal-tentorial, stipital-tentorial, lacinial-cranial, and lacinial-stipital muscles are visible at all stages of development. The galeal-stipital, the both palpal-stipital and the single palpal muscles are not seen when larva transforms to pupa (Fig. 19), but they have identical arrangement in larval and pupal-imaginal maxilla (Figs 18, 20). In larva the galeal-stipital muscle passes through the common base of galea and palp, and the single palpal muscle locates in the same common base (Fig. 18). In pupa and imago the galeal-stipital muscle passes through a separate galeal pedestal (Fig. 20). This means that the galeal pedestal, which in pupa and imago is a separate projection of stipes, in larva is completely fused with the 1st segment of palp to form something like a segment.

(2) Maxillary setation is identical in larva and pupa (Figs 18, 20), but imago has numerous additional setae which mask the primary ones. There are following primary (larval-pupal) setae: 1 long seta on ventral surface of cardo; 6 long setae on lateral side of stipes; 1 seta on base of lacinia; 5 setae on biting edge of lacinia (3 dorsal, 1 ventral and 1 apical); 1 seta on midlength of galea; some minute

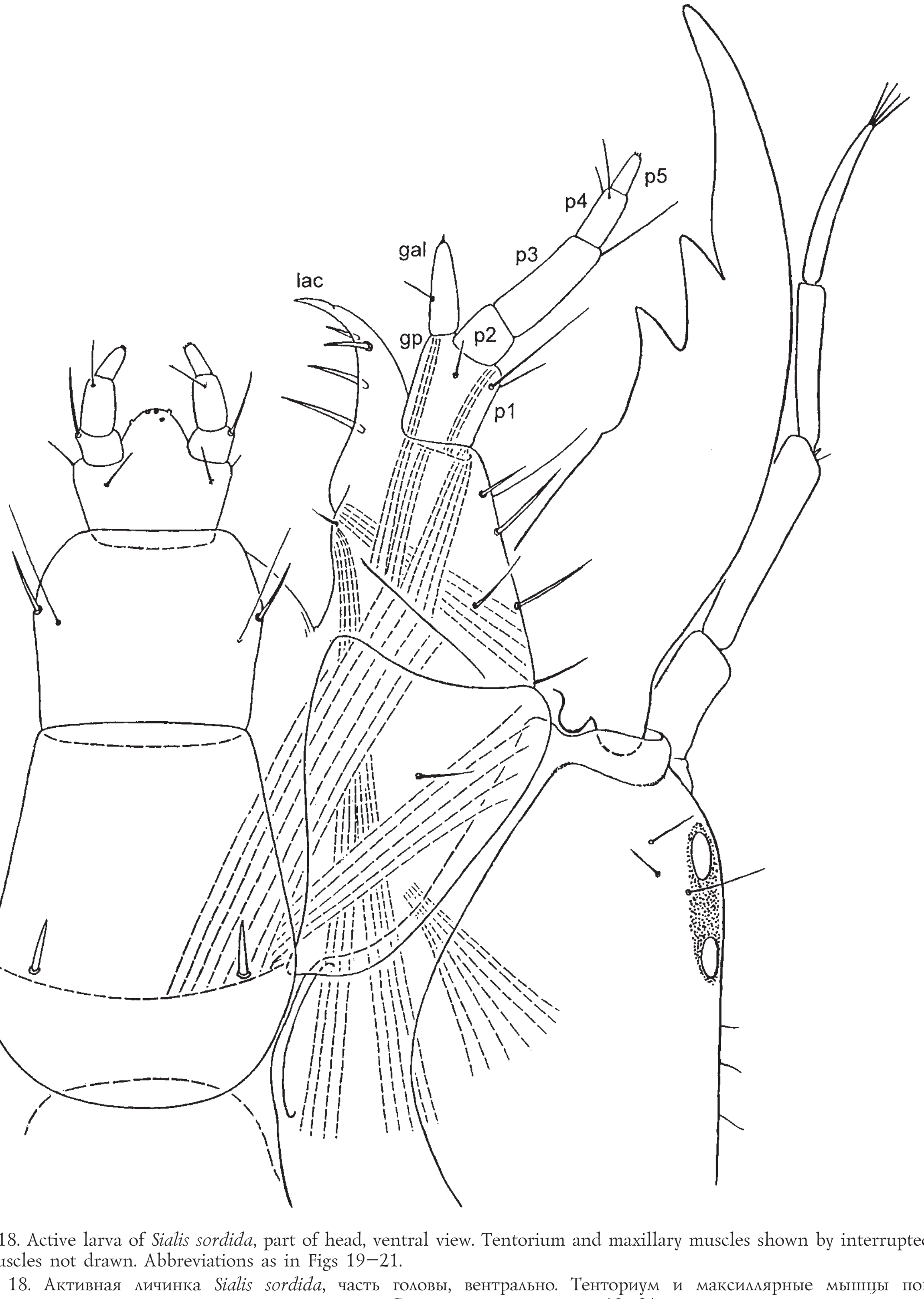
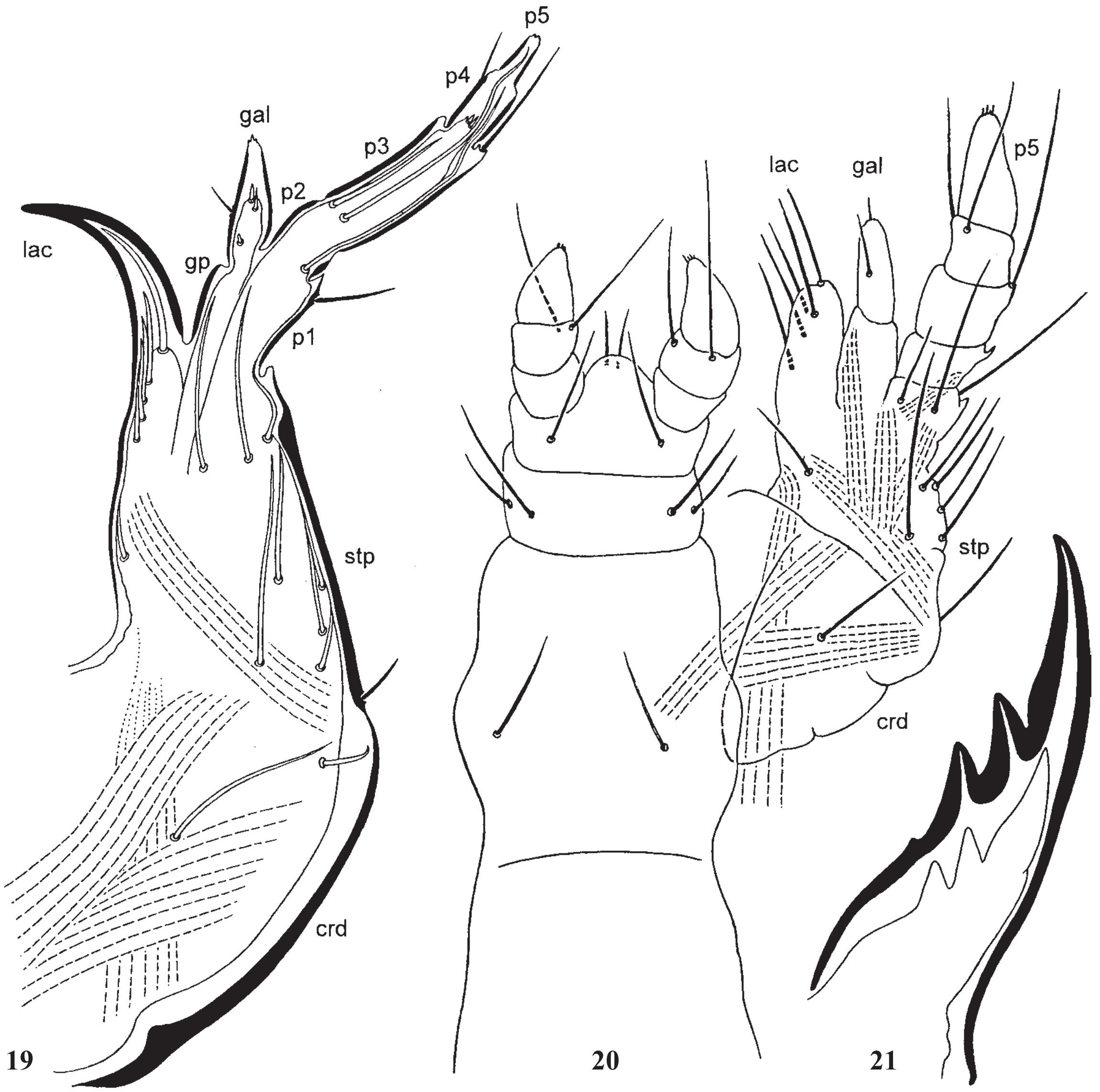


Fig. 18. Active larva of *Sialis sordida*, part of head, ventral view. Tentorium and maxillary muscles shown by interrupted lines; other muscles not drawn. Abbreviations as in Figs 19–21.

Рис. 18. Активная личинка *Sialis sordida*, часть головы, вентрально. Тенториум и максиллярные мышцы показаны прерывистыми линиями; другие мышцы не показаны. Сокращения как на рис. 19–21.

apical galeal setae; 3 setae on 1st palpal segment; 1 seta on lateral side of 3rd palpal segment; 2 setae on medial side of 4th palpal segment; some minute apical setae on apex of 5th palpal segment. In pronymphal phase pupal setae are visible through larval cuticle, and the setation allows to see how pupal parts are shifted proximally relatively to the homologous larval parts.

(3) At early stage of development of the pupal maxilla under larval cuticle, tips of pupal lacinia, galea and palp remain inside the homologous larval appendages (Fig. 19); this helps to find correct correspondence between the larval and the pupal-imaginal parts. At later stage, the pupal lacinia, galea and palp are shifted more proximally and become crumpled inside the larval sti-



Figs 19–21. *Sialis sordida*: 19 — maxilla of pronymph, optic section (larval cuticle shown by black as optic section; future pupal maxilla shown as ventral view; retained and partly degenerated muscles shown by interrupted and dotted lines correspondingly); 20 — labium and maxilla of pupa, ventral view (maxillary muscles shown by interrupted lines, other muscles not drawn); 21 — mandible of late pronymph, optic section (larval cuticle shown by black as optic section; outline of future pupal mandible shown by thin line). Abbreviations: crd — cardo; gal — galea; gp — galeal pedestal (distal outgrowth of stipes) adhered to first segment of maxillary palp; lac — lacinia; p1, p2, p3, p4, p5 — 1st–5th segments of maxillary palp; stp — stipes.

Рис. 19–21. *Sialis sordida*: 19 — максилла пронимфы, оптический срез (личиночная кутикула показана черным как оптический срез; будущая куколочная максилла показана с вентральной стороны; сохранившиеся и частично дегенерировавшие мышцы показаны прерывистыми и пунктирными линиями соответственно); 20 — нижняя губа и максилла куколки, вентрально (максиллярные мышцы показаны прерывистыми линиями; прочие мышцы не нарисованы); 21 — мандибула поздней пронимфы, оптический срез (личиночная кутикула показана черным как оптический срез; очертание будущей куколочной мандибулы показано тонкой линией). Сокращения: crd — кардо; gal — галеа; gp — постамент галеи (дистальный вырост стипеса), проросший к первому членику максиллярного щупика; lac — лациния; p1, p2, p3, p4, p5 — 1–5-й членики максиллярного щупика; stp — стипес.

pes, thus the larval cuticular lacinia, galea and palp appear to be empty.

As can be seen, the larval segment, which looks as a common base for galea and palp, is actually a result of fusion of the first segment of palp with a galeal pedestal (a projected portion of stipes, to which galea is attached). Thus, 4-segmented larval palp consists of initial palp segments 2–5. In pupa and imago first segment of palp is free, and the palp has normal 5-segmented structure.

MANDIBLE. Pupal mandibles are functional; mandibles retain functional musculature during all metamorphosis (unlike Birostrata). At pronymphal phase, the future pupal mandible locates inside the larval cuticular mandible in such a way, that apex of pupal incisor lies inside apex of larval incisor (Fig. 21) (unlike Birostrata,

whose apices of larval and pupal mandibles are different — see above).

1.3.2. **Eumegaloptera**

Circumscriptional name: **Eumegaloptera** Riek, 1974.
Hierarchical name: **Corydalus/f2=Chauliodes/g2** (sine *Sialis*).
Typified names in use: **Corydalida**, **Corydalidae**, **Corydalinae**, **Chauliodidae**.

AUTAPOMORPHIES OF EUMEGALOPTERA. Larval pygopod is transformed to a pair of leg-like projections, each with two apical claws and a lateral gill appendage. At all stages (larva, pupa and imago) head has a large gula (but unlike Rhaphidioptera, retains strongly developed tentorium). Maxilla is modified: larval, pupal and imaginal stipes is strongly elongate and cylindrically projected (but, unlike Rhaphidioptera, without a median wall proximad of lacinia); larval (but not pupal and imaginal) lacinia is lost, being completely fused with stipes (similar to Rhaphidioptera).

External structure of mouthparts of larva, pupa and imago, and musculature of larva and imago of *Corydalus cornutus* are adequately described and figured by Kelsey [1954].

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